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OSTEOLOGY AND DESCRIPTION OF *THRATTIDION NOCTIVAGUS*, A MINUTE, NEW FRESHWATER CLUPEID FISH FROM CAMEROON, WITH A DISCUSSION OF PELLONULIN RELATIONSHIPS

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ABSTRACT. *Thrattidion noctivagus*, a new genus and species of Pellonulinae, is described from the Sanaga River in Cameroon, and an account given of its osteology. Although it agrees with *Congothrissa* in having no supramaxillary bone, the two appear not to be closely related. The ecology of African freshwater Pellonulinae is reviewed. Feeding habits range from planktophagous to insectivorous and piscivorous, with piscivores feeding largely on other species of Pellonulinae. Most or all of the species undergo diel migrations, moving upwards or shorewards at nightfall in mixed aggregations with other small fishes, chiefly translucent schilbeid catfishes and cyprinids of the subfamily Bariliinae.

Sierrathrissa Audenaerde (1969) is evidently the larva of either *Pellonula* or *Cynothrissa*. *Congothrissa* Poll (1964) is referred to the Pellonulinae. Relationships of round herrings (Dussumieriidae) that seem close to Pellonulinae are also discussed; *Laeviscutella* should be placed in the Pellonulinae.

INTRODUCTION

During fieldwork on the Sanaga River in Cameroon, I collected a minute clupeid which is clearly a member of the Pellonulinae but defies placement in any described genus. In lacking a supramaxillary bone in the upper jaw it differs from all other known clupeoids excepting *Congothrissa* (Poll, 1964) from the Congo basin. Consequently the distinctions between *Congothrissa* and

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other clupeids are not so great as they at first appeared, and it may now be referred with some confidence to the Pellonulinae. Nevertheless these two minute clupeids are not more closely related to each other than to other forms, and their relationships within the Pellonulinae are unclear. The description of this new form from Cameroon is accompanied by an account of its osteology in the hope that this will contribute to its eventual placement in a phyletic classification.

Acknowledgments. I wish to thank Mr. Thomason Newcomb for providing a congenial lodging place during my stay at Edea, and Prof. George S. Myers for reading the manuscript. The fieldwork was assisted financially by the Office of Environmental Sciences (contract no. RC 717634).

THRATTIDION, new genus

Type species. Thrattidion noctivagus, new species.

Diagnosis. Minute (largest specimen 21.4 mm), largely translucent Pellonulinae with direct development. Four to seven keelless prepelvic abdominal scutes and three to five (usually four) strongly keeled postpelvic abdominal scutes. All scutes with well-developed lateral (ascending) arms; pelvic scute with bifurcate or trifurcate lateral arms in larger specimens.

Supramaxillary bones absent. Maxillary toothless. Branchiostegal rays 5,5 or 5,4. Lower limb of first gill arch with 10–11 and upper limb with four short, widely spaced gill rakers.

Anal fin considerably longer than dorsal, with 23–25 rays. Origin of dorsal fin about one-third of distance between verticals through pelvic and anal fin origins. Origin of anal fin on a vertical through base of eighth or ninth dorsal fin ray. Pectoral rays usually ten.

Squamation restricted to a patch of about a dozen scales just behind head, a double row of scales on either side of prepelvic abdominal scutes, and a single row of scales on either side of postpelvic abdominal scutes. Vertebrae 45–47, about equally divided between abdominal and caudal (preural centrum 1 counted as last vertebra). Epurals three.

Remarks. If the largest specimens in my material are fully grown, *Thrattidion* is the smallest clupeoid yet described. Next smallest is *Congothrissa,* with specimens recorded up to 27.7 mm (here and throughout this paper lengths referred to are standard lengths). Almost all African freshwater clupeids have nine or more prepelvic scutes and at least seven postpelvic scutes; in these forms the prepelvic as well as postpelvic scutes are invariably serrated or keeled. The only exceptions from freshwater in Africa are 1) *Congothrissa,* which lacks abdominal scutes entirely except for a pelvic scute; 2) *Laeviscutella,* with seven to eight keel-less prepelvic scutes and five to six keeled postpelvic scutes; and 3) *Gilchristella,* with six to nine unkeeled prepelvic scutes and no postpelvic scutes. The postpelvic scutes in *Laeviscutella* are unique in lacking lateral arms as adults (lateral arms are, however, absent in the postpelvic scutes of larval *Pellonula*). The lateral arms of the pelvic scutes are usually simple; they are bifurcate in *Congothrissa* (Poll, 1964, fig. 5 on p. 14).

All previously described clupeoids have one or two supramaxillary bones except *Congothrissa.* Pellonulinae characteristically have only one supramaxillary bone (Regan, 1917); its presence has been noted in alevins of *Poecilothrissa moeruensis, Stolothrissa tanganicae* and *Microthrissa stappersii* so small that the abdominal scutes are as yet unformed (Poll, 1964: 19). The supramaxillary is reduced in size in some Pellonulinae. The maxillary bone bears teeth in all other African freshwater clupeoids except *Congothrissa* and *Potamothrissa.* Most African freshwater clupeids have 6,6 or more branchiostegal rays; *Poecilothrissa, Microthrissa* and *Potamothrissa* have as few as five; *Congothrissa* has 3,4 (here as elsewhere in this paper, the count on the left side is given first). All other African clupeoids have 16 or more gill rakers on the first gill arch, excepting *Congothrissa,* which has only seven on the lower limb and four on the upper limb of the first arch.

All other African Pellonulinae have 23 or fewer anal rays, except *Microthrissa,* which has up to 25. *Congothrissa* has only 15. In *Congothrissa* the dorsal fin origin is distinctly anterior to a vertical through origin of pelvic fins. In almost all African freshwater clupeids the anal fin origin is far behind a vertical through base of last ray of anal fin, the exceptions being larval *Pellonula,* in the metamorphosis of which the dorsal fin migrates forward, and *Microthrissa* and *Gilchristella,* in which the anal fin origin is on or only slightly posterior to a vertical through the last ray or two of the dorsal fin. In larval *Pellonula* the anal fin origin may be as far forward as posterior third of dorsal fin. All other African freshwater clupeoids have 11 or more pectoral rays.

In all other African clupeoids the body is completely scaled in adults; the highest vertebral count previously recorded is 44, with abdominal vertebrae usually more numerous than caudal (Poll, 1964, table 1). *Congothrissa* has 21+20 vertebrae. The number of epurals is unrecorded for most Pellonulinae; *Congothrissa* and larval *Pellonula* have two epurals.

Etymology. Thrattidion, Greek, neuter diminutive of Thrassa (Thratta), feminine, a small, herringlike fish.

Thrattidion noctivagus, new species
Figures 1 and 2; Table 1

Holotype. MCZ 48161, 21.4 mm, Sanaga River at Edea, Cameroon, 4 May 1971.

Paratypes. MCZ 48162, 175 specimens, 9.8–20.7 mm (of which 11 specimens 10.4–20.7 mm cleared and stained), Sanaga River at Edea, 17 April and 4 May 1971.

The specimens are in excellent condition. They were fixed in formalin immediately after capture and placed in Nalgene plastic bottles containing only small specimens and filled to the brim to prevent damage by shaking. Consequently, the fins are in perfect condition on almost all specimens, and the squamation completely intact. After three months in formalin they were soaked in water for two days, in 40 percent ethyl alcohol for two more days, then transferred to 70 percent ethyl alcohol for permanent preservation.

General characteristics. Snout short and rounded. Jaws equal. Body relatively compressed, depth 3.55–5.0, increasing with size.

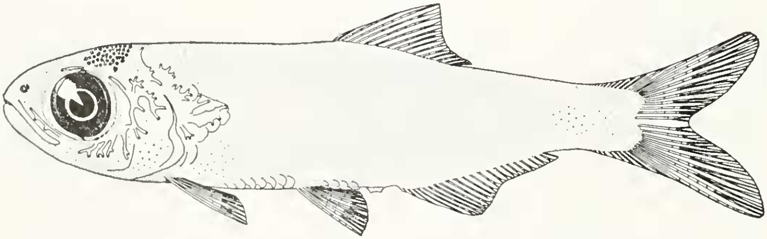

Figure 1. *Thrattidion noctivagus,* 19.4-mm paratype. MCZ 48162.

Eye large, 8.5–9.9, its center on or only slightly above longitudinal midline of body (center of eye distinctly above midline in most Pellonulinae, markedly so in *Odaxothrissa* and *Cynothrissa*). Adipose eyelid well developed. Dorsal fin origin distinctly posterior to a vertical through pelvic origin, slightly closer to end of hypural fin than to snout tip. Anal fin long, its origin on a vertical through base of eighth or ninth dorsal fin ray.

Pelvic, dorsal, and anal origins on verticals through 15th, 19th, and 25th vertebrae. Pelvic fin relatively large, only slightly smaller than pectoral, its origin closer to pectoral fin origin than to anal fin origin. Dorsal and anal fin margins gently falcate, dorsal height about 1.5 times anal height. Caudal fin deeply forked, upper and lower caudal lobes identical in size and shape.

For proportional measurements see Table 1.

Fin counts (Table 1). Dorsal fin with 14–16 rays, first three or four simple, last divided to base. Anal fin with 23–25 rays, first four or five simple, last divided to base. Length of first dorsal and anal rays variable, minute in some specimens. Pectoral fins usually with ten rays. Pelvic fins with either seven or eight rays. Principal caudal rays invariably 10+9, upper procurrent rays 12–13 and lower procurrent rays eight to ten.

Squamation (Fig. 1). Scales largely absent, restricted to a double row of four to nine scales superficial to lateral arms on each side of prepelvic scutes, a single row of four or five scales superficial to lateral arms on either side of postpelvic scutes, and about a dozen scales in four or five short rows immediately behind head. The latter scales are deeply embedded in tough tissue in which the trunk portion of the cephalic laterosensory system ramifies, and can only be fully discerned in cleared and stained specimens. A 20.7-mm specimen has 12 scales in four rows (three in the uppermost row, five in the second row, one in the third row, and three in the lowermost row); a 19.1-mm specimen 11 scales in five rows (2–4–1–3–1); and an 18.6-mm specimen 11 scales in five rows (1–2–4–2–2). Most of the scales in the longest row are perforated by laterosensory canals. Larval *Pellonula* of 36–38 mm have the body naked except for two or three scales immediately behind the head and complete squamation on the caudal peduncle.

Standard length	Holotype 21.4 mm	20.7 mm	20.0 mm	Specimen in Fig. 1 19.4 mm	19.1 mm	Specimen in Fig. 13 18.6 mm	17.8 mm	17.1 mm	15.8 mm	14.3 mm	12.1 mm	11.0 mm	10.4 mm	Range, Frequency, or Comment
Head	3.6	3.7	3.9	3.6	3.7	3.65	3.56	3.6	3.6	3.6	3.7	3.55	3.7	3.55-3.9
Eye	9.7	9.9	9.5	9.0	9.1	8.9	9.4	9.5	9.0	9.5	9.3	8.5	9.0	8.5-9.9
Snout	13.4	16.0	16.6	13.8	17.4	14.3	14.2	12.2	14.4	13.0	15.2	12.2	13.0	12.2-17.4
Depth	3.55	4.1	4.0	4.1	3.9	4.15	4.35	4.3	4.3	4.3	4.65	5.0	4.7	3.55-5.0
Snout-dorsal origin	1.86	1.90	1.85	1.86	1.87	1.86	1.87	1.88	1.88	1.90	1.86	1.82	1.79	1.79-1.90
Snout-anal origin	1.60	1.55	1.66	1.58	1.54	1.54	1.60	1.56	1.56	1.55	1.60	1.60	1.55	1.54-1.90
Snout-pelvic origin	2.04	2.10	2.08	2.06	2.03	2.10	2.06	2.08	2.05	2.07	2.09	2.04	1.98	1.98-2.10
Depth caud. ped.	8.9	9.0	9.1	9.5	9.1	9.3	9.1	9.0	9.3	8.9	9.7	10.0	9.0	8.9-10.0
Length caud. ped	6.5	7.1	6.9	6.8	7.35	7.45	7.1	7.4	7.0	7.15	6.05	6.5	6.9	6.05-7.45
Pect. length	5.5	5.8	5.6	5.4	5.5	5.3	5.4	5.5	5.45	6.0	-	5.7	-	5.3-6.0
Pelvic length	6.9	7.1	6.4	6.7	7.6	7.15	7.7	6.8	6.9	7.15	-	6.5	-	6.5-7.6
Anal base	3.7	3.8	4.0	4.05	4.0	3.9	3.8	4.0	3.6	3.8	4.7	5.65	4.0	3.6-5.65
Prepelvic scutes	-	5	7	-	7	4	6	6	4	6	4	-	4	4-7
Postpelvic scutes	-	4	5	-	4	4	3	4	4	4	4	-	2	3-5
Branchiostegal rays	-	5,5	5,4	-	5,5	5,5	5,5	5,4	5,5	5,5	5,5	-	1,4	5,5(7), 5,4(2), 1,4(1)
Gill rakers	-	5+11	-	-	-	5+11	-	-	-	-	-	-	-	5+11
Supraneurals	-	10	12	-	12	11	11	11	10	12	0	-	0	10-12
Epurals	-	3	3	-	3	3	3	3	3	3	3	-	3	3
Vertebrae	-	47 (24+23)	45 (23+22)	-	46 (23+23)	45 (23+22)	47 (23+24)	45 (22+23)	45 (23+22)	47 (23+24)	46 (23+23)	-	46 (23+23)	45(4), 46(3), 47(3)
Dorsal fin	iv 11	iii 12	iii 12	iv 12	iv 11	iii 12	iii 11	iii 11	iv 10	iv 11	-	-	-	14(3), 15(6), 16(1)
Anal	v 18	iv 19	v 18	v 18	v 18	iv 19	iv 21	iv 19	iv 20	v 19	-	-	-	23(6), 24(3), 25(1)
Pectoral	10,10	10,10	10,10	10,10	10,10	11,11	10,10	9,10	10,10	10,10	10,9	-	-	usually 10,10
Pelvic	8,8	8,8	7,7	8,8	7,7	8,8	8,8	8,8	7,7	7,7	7,7	-	-	7,7(5), 8,8(6)
Caudal	12X-IX10	12X-IX9	12X-IX10	12X-IX9	12X-IX8	12X-IX9	12X-IX10	12X-IX10	12X-IX10	13X-IX10	9X-IX8	-	2X IX1	most often 12X-IX10

TABLE 1. Thrattidion noctivagus. Proportions expressed as times in standard length, fin ray counts, and other counts. In counts of branchiostegal rays and pectoral and pelvic fin rays, first numeral is for left side, second numeral for right side.

Cephalic laterosensory system (Fig. 2). Cephalic laterosensory system with supraorbital, infraorbital, mandibulo-preopercular, pterotic, opercular, occipital and lateral canals (cf. Wohlfahrt, 1937). A supratemporal branch arises from the supraorbital; in some specimens it appears to enter the occipital canal, but in others it definitely stops short of reaching the occipital canal. Figure 2 is based on a 15.1-mm specimen that had a drop or two of Ehrlich's hematoxylin placed on its head. Of several specimens thus treated, its canals showed up the best. The mandibular portion of the mandibulo-preopercular canal could not be distinguished on this specimen, but it appeared in others. The main canals appear to join in the manner illustrated, but the figure should be used with caution. The canals did not take up stain evenly, and comparisons with less well-stained specimens did not eliminate my reservations about the interpretation. I could find no connections between the laterosensory systems of the two sides of the head. In particular the ethmoidal commissure is absent.

Dentition. Premaxillary with four to seven small conical teeth solidly implanted, and two to four replacement teeth in the gum.

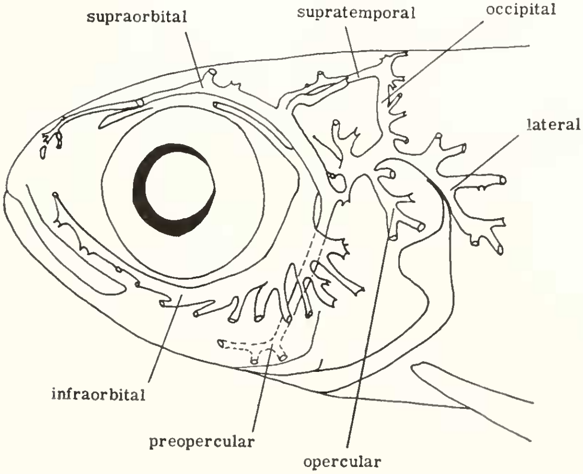

Figure 2. *Thrattidion noctivagus,* cephalic laterosensory canals of 15.1-mm paratype.

Maxillary edentulous. Dentary with a dozen to 15 small conical teeth solidly implanted and several teeth in stages of replacement. Palatine with one to three teeth, roof of mouth otherwise edentulous. Fifth ceratobranchial and upper pharyngeal with numerous small teeth, gill arches otherwise edentulous.

Abdominal scutes. Four to seven prepelvic scutes, unkeeled, with well-developed lateral arms. Pelvic scute keel-less, with bifurcate or trifurcate lateral arms in largest specimens. Postpelvic scutes three to five, usually four, with well-developed keels and lateral arms. Specimens as small as 12–14 mm with full complement of scutes (Table 1).

Coloration of preserved specimens. Body opaque white, without melanophores, or with only a few melanophores in some specimens at base of anal fin rays and on caudal peduncle. No lineum argenteum. Peritoneum probably opaque white and body otherwise translucent in living specimens. A dense cluster of large melanophores over brain. Specimens were collected only at dusk or at dawn and immediately preserved, so observations were not made on their appearance in life.

Additional characteristics. See generic diagnosis and osteological account.

OSTEOLOGY

Neurocranium (Figs. 3–5). Anterior and posterior frontal fontanelles very large. Anterior margin of anterior frontal fontanelle formed by diverging posterior arms of mesethmoid. Posterior frontal fontanelle incompletely divided into right and left halves, the median extension of supraoccipital failing to reach posteromedial border of frontal bones. Of the types of clupeoid posterior frontal fontanelles figured by Whitehead, those of *Spratelloides* and *Ehirava* (Whitehead, 1963a, fig. 1) resemble most closely that of *Thrattidion.* As in *Ehirava,* a median extension of the frontals forms a distinct wedge in the posterior frontal fontanelle. Frontals slightly separated at midline of skull. Anterior fontanelle about half as wide as posterior fontanelle.

Mesethmoid solidly ossified, with well-developed anterolateral and descending processes, and diverging posterior processes firmly united to anterior ends of frontal bones. Lateral ethmoid with a large cartilaginous portion ventrally.

Pre-epiotic fossa large, an anteroventrally directed process of parietal bone only partially separating it from temporal foramen. Pre-epiotic fossa bordered mainly by frontal and parietal; temporal foramen bordered by parietal, epiotic and pterotic (Fig. 3).

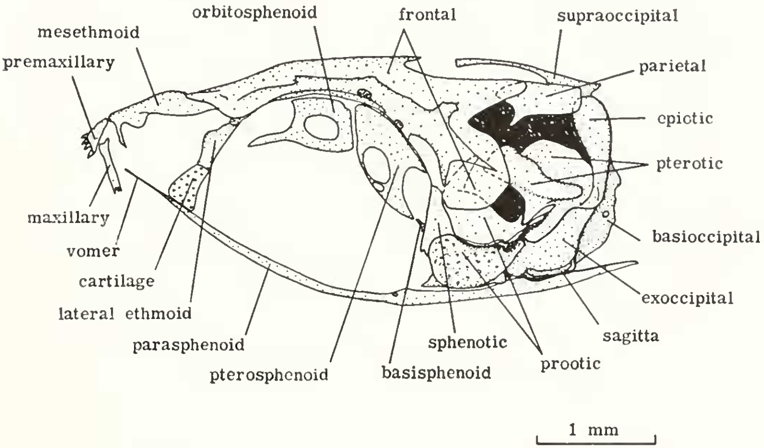

Figure 3. Cranium of 18.6-mm *Thrattidion noctivagus,* lateral view.

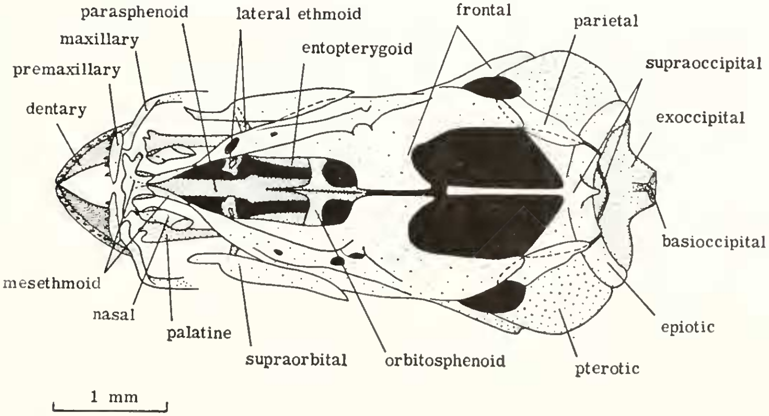

Figure 4. Cranium of 20.0-mm *Thrattidion noctivagus,* dorsal view.

A large foramen bordered by the frontal, pterotic, and prootic opens into the recessus lateralis (Fig. 3). It seems likely that all of the main branches of the cephalic laterosensory system enter the recessus through this one large opening. A laterally directed ridge on prootic extending onto anteroventral portion of pterotic, both bones apparently contributing to this ridge posteriorly.

Intercalar bone present, a small, oval bone lying in the interosseous membrane between exoccipital, pterotic, and prootic, its edges touching each of these bones (Fig. 5). When the pectoral girdle is removed from the skull, the intercalar is invariably carried away with the lower limb of the posttemporal bone.

I am unable to find a passageway through which anterior extensions of the swim bladder might gain the prootic bulla. A small oval opening in the exoccipital bone opens into a passageway directed dorsoposteriorly, away from the prootic. This opening and its passageway do not have counterparts in the prootic. The opening is flush with the exoccipital, not funnel-shaped as one would expect of an opening for the swim bladder; it probably serves for passage of cranial nerves. A large dorsal foramen of the prootic is readily visible.

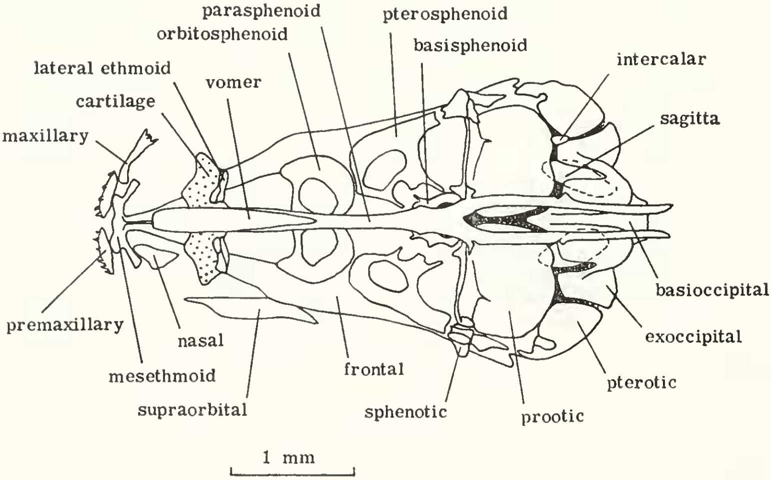

Figure 5. Cranium of 18.6–mm *Thrattidion noctivagus,* ventral view.

Orbitosphenoid, pterosphenoids, and basisphenoid well developed, with large lateral foramina. Orbitosphenoid with an anteriorly directed process.

Vomer edentulous, elongate, and flattened. Parasphenoid uniformly slender, dividing where it meets base of neurocranium into a pair of posterior processes, the tips of which extend beyond occiput to immediately below second or third vertebral centrum (Fig. 5).

Jaws (Figs. 6–7). Premaxillaries separated at midline, each bearing four to seven conical teeth. Maxillary relatively slender, extending to below anterior third of eye, toothless. Supramaxillaries absent. Dentary with a low coronoid process and a single row of about a dozen to 15 conical teeth. Articular with a posteriorly directed process posterior to quadrate socket.

Suspensorium (Fig. 7). Palatine bifid at its tip, bearing one to three conical teeth. Suspensorium otherwise edentulous. Ectopterygoid slender anteriorly, moderately expanded where it

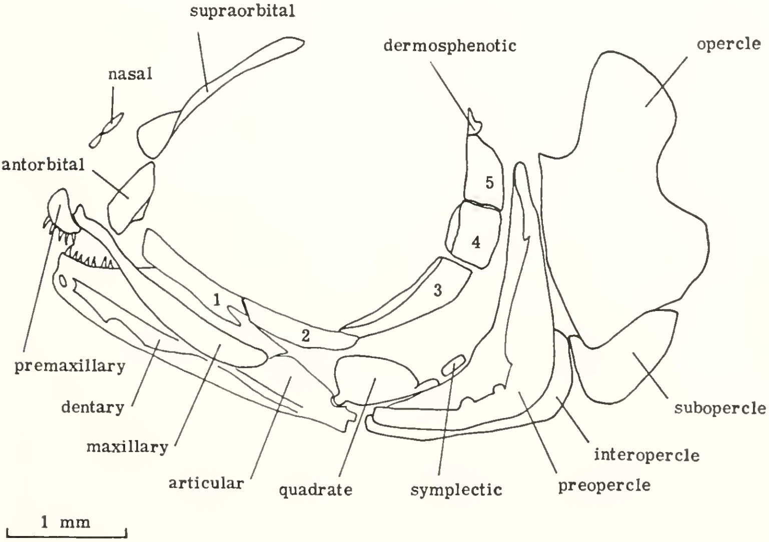

Figure 6. Jaws and facial bones of 20.7-mm *Thrattidion noctivagus,* lateral view (1–5 = circumorbital bones).

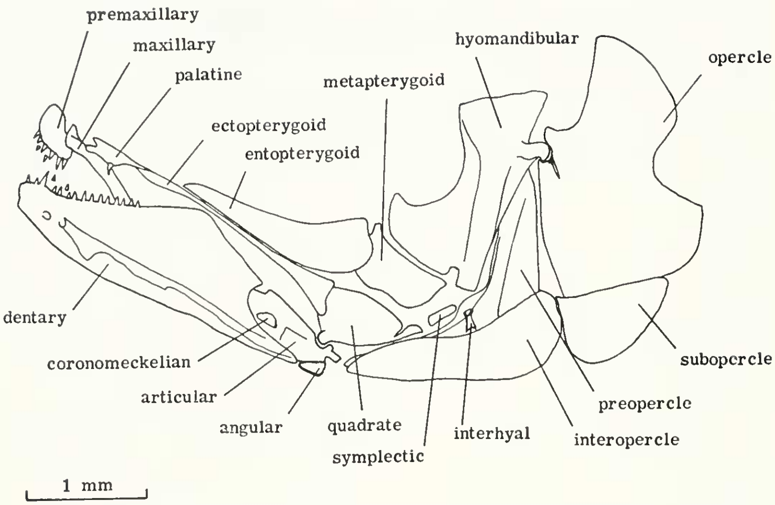

Figure 7. Jaws, suspensorium, and opercular bones of 20.7-mm *Thrattidion noctivagus,* medial view.

attaches to dorsoanterior portion of quadrate bone. Entopterygoid and metapterygoid well developed. Sphenotic and pterotic articular surfaces of hyomandibular not strongly differentiated from its main body. Hyomandibular with a distinctively shaped lamella dorsoanterior to its symplectic process, the ventral margin of this lamina separated from symplectic process of hyomandibular by a notch. Symplectic bone relatively small, lying midway between hyomandibular and quadrate but in contact with neither. Quadrate with a posterior process directed towards anterior end of symplectic.

Facial bones (Fig. 6). Circumorbital series with an antorbital followed by six infraorbitals, a pattern found in generalized members of many teleostean groups, including Clupeomorpha (Nelson, 1969). Dermosphenotic greatly reduced. Infraorbitals shallow, without extensive ventral laminae. Supraorbital bone large and elongate.

Nasal bones widely separated, moderate in size, bearing a tube for laterosensory canal.

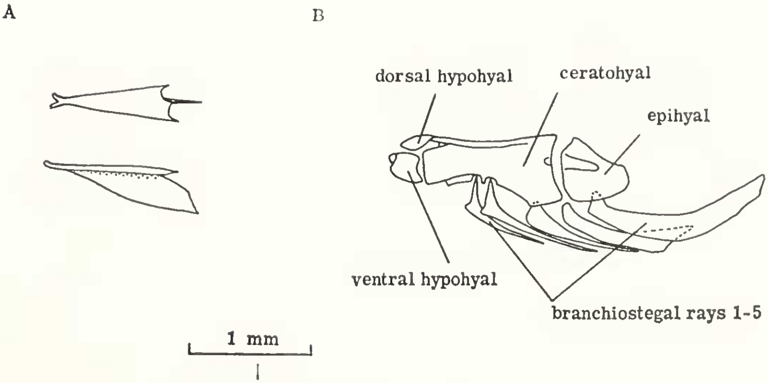

Figure 8. A. Urohyal bone (upper: dorsal view; lower: left lateral view); and B. hyoid arch (basihyal and interhyal removed), lateral view, of 20.7-mm *Thrattidion noctivagus.*

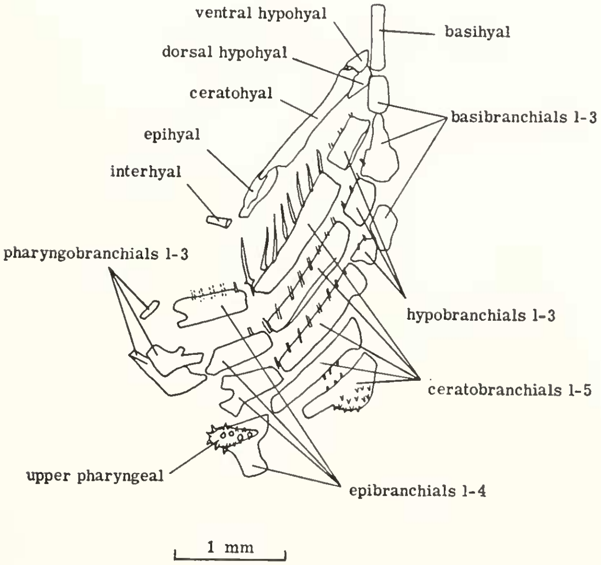

Figure 9. Hyoid arch (branchiostegal rays removed) and branchial arches of left side, of 20.7-mm *Thrattidion noctivagus.* Dorsal view, upper limb of gill arches unfolded and pinned to the side.

Opercular series complete; dorsoanterior corner and posterior margin of opercle deeply incised.

Hyoid and branchial arches (Figs. 8–9). The branchial skeleton of *Thrattidion* differs from that in most clupeids in several respects; this is perhaps mainly due to its reduced size. Gill rakers and pharyngeal dentition reduced. Branchial skeleton lacking elongation of individual parts typical of most living clupeoids (and which is at least partly correlated with increased numbers of gill rakers and branchiostegal rays). Basihyal well ossified and toothless (usually cartilaginous and tooth-bearing in Pellonulinae, Nelson, 1967: 393). Pharyngeal teeth restricted to upper pharyngeal and ceratobranchial 5. Gill rakers few in number, widely spaced, and relatively short. The 20.7-mm specimen represented in Figure 9 has 15 rakers on the first gill arch, including a few that are rudimentary or unossified. Gill rakers progressively reduced in size and number on arches 2–5.

The hyoid arch has paired ventral and dorsal hypohyals, ceratohyal, epihyal and interhyal, and a median basihyal. Branchiostegal rays 5,5 in eight specimens, 5,4 in two; generally one branchiostegal ray attached to epihyal, three to ceratohyal, and one branchiostegal ray in between, not attached to either bone.

Individual ossified parts of the branchial arches are median basibranchials 1–3, and paired hypobranchials 1–3, ceratobranchials 1–5, epibranchials 1–3, suspensory pharyngeals or infrapharyngeals 1–3, and upper pharyngeals.

Pectoral girdle (Fig. 10). Two slender postcleithra, distal end of second postcleithrum attached by ligament to distal end of first rib. Four proximal radials and about six distal radials (distal radials absent in clupeoids other than Chirocentridae, according to Whitehead, 1963a and Greenwood, 1968). Other bones in pectoral girdle: extrascapular, posttemporal, cleithrum, coracoid, scapula, mesocoracoid.

Pelvic girdle (Fig. 11). Pelvic bones relatively elongate and slender. Articular portion of pelvic bone with a deep, elongate notch. Three pelvic radials. Pelvic splint present (pelvic splint absent in clupeoids, according to Whitehead, 1963a and Greenwood, 1968).

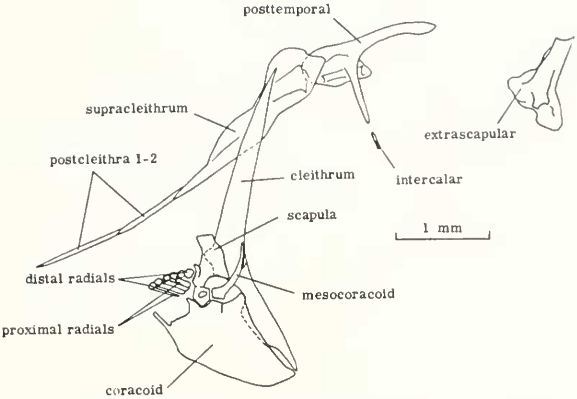

Figure 10. Pectoral girdle of 20.7-mm *Thrattidion noctivagus,* medial view. Inset, upper right hand corner: extrascapular bone of same specimen, lateral view.

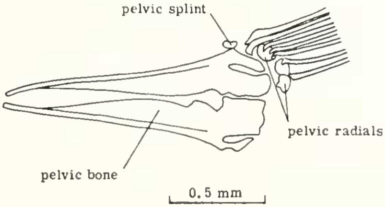

Figure 11. Pelvic girdle of 18.6-mm *Thrattidion noctivagus,* dorsal view.

Abdominal scutes (Fig. 12). Prepelvic scutes four to seven, keel-less, with slender lateral arms. Pelvic scute enlarged, with bifurcate or trifurcate lateral arms in larger specimens (specimen figured has two branches on one side, three on the other). Postpelvic scutes usually four, invariably with well-developed keels. Specimens only 12.1 and 14.3 mm have a full complement of pelvic scutes (Table 1). In a 10.4-mm specimen only the pelvic scute is visible. In a 12.1-mm specimen the scutes are represented only by the lateral arms, which ossify separately. With growth they fuse to form a median scute. In the middle of the scutes in larger specimens is sometimes a foramen or gap in the ossification where the two halves are incompletely fused, as in the second three prepelvic scutes in the 20.7-mm specimen figured.

Vertebral column and associated bones (Fig. 13). In a series of ten specimens the vertebral count ranges from 45 to 47; abdominal and caudal vertebrae about equal in number. The counts and their frequencies are 22+23 (1); 23+22 (3); 23+23 (3); 23+24 (2); and 24+23 (1). The third vertebra is the first to bear ribs. The tips of ribs 4–7 to 2–9 are bound by connective tissue to the lateral arms of the prepelvic scutes; rib 9 or 10 to the pelvic scute, and ribs 10 or 11 through 15 to the postpelvic scutes.

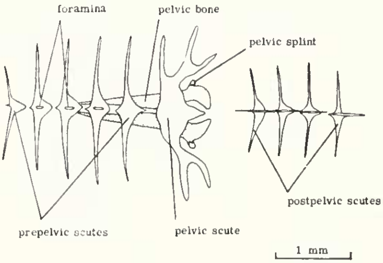

Figure 12. Abdominal scutes of 20.7-mm *Thrattidion noctivagus,* ventral view.

There are four distinct sets of intermuscular bones: 1) epaxials or epineurals, 2) epicentrals, 3) anterior hypaxials or epipleurals, and 4) posterior hypaxials. The epaxials begin at about the eighth vertebra and continue to the second preural centrum. The epicentrals begin at the first vertebra and continue to the second preural centrum. The epicentrals begin at the first vertebra and extend to about the first caudal vertebra. The anterior hypaxials or epipleurals begin at the second vertebra and extend to the last abdominal vertebra. The posterior hypaxials begin at about the fourth or fifth caudal vertebra and extend to about the second preural centrum. All of the intermuscular bones are relatively simple; in particular the epicentrals, epaxials, and posterior

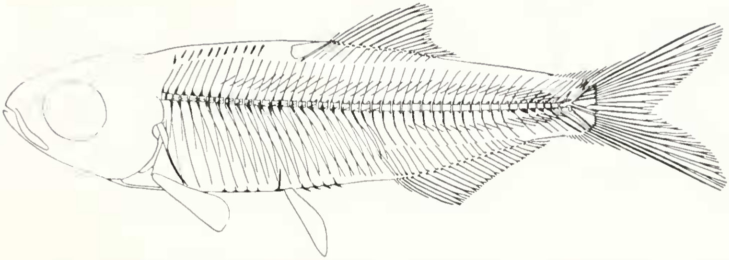

Figure 13. Axial skeleton of 18.6-mm *Thrattidion noctivagus*, lateral view.

hypaxials are unbranched. The anterior hypaxials are almost as long as the ribs and are expanded near their proximal ends into a triangular lamella.

There are ten to twelve supraneural bones. The first supraneural lies just dorsal to the first neural spine; the last lies over the tenth to twelfth neural spine.

Caudal skeleton (Fig. 14). Caudal skeleton with six hypurals, hypural 1 separated from ural centrum 1 by a distinct gap. Preural centrum 1, ural centrum 1 and ural centrum 2 fused.

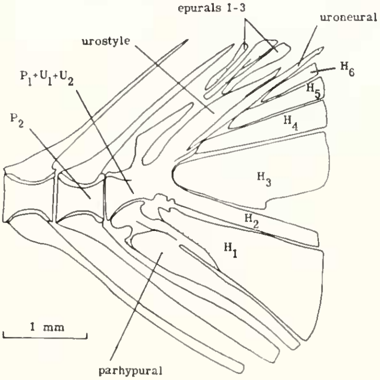

Figure 14. Caudal skeleton of 20.7-mm *Thrattidion noctivagus*, lateral view ($H_1 - H_6$ = hypurals; $P_1 + U_1 + U_2$ = fused preural centrum 1, ural centrum 1 and ural centrum 2; P_2 = preural centrum 2).

Hypural 2 fused with ural centrum 1. Parhypural (= hemal spine of preural centrum 1) closely articulated with centrum of preural centrum 1, its dorsal margin with a very large, laterally directed flange or hypurapophysis. The single uroneural lies free against the ural spine and does not extend anteriorly to the ural centrum 1. Epurals three.

Caudal fin lobes almost perfectly symmetrical. Principal caudal rays invariably ten in upper lobe and nine in lower lobe. Specimens 14 mm upwards have 12 or 13 upper and eight to ten lower procurrent rays, all of which take up alizarin stain. Hypurals 1 and 3 expanded, hypural 2 slender. Hypural 1 articulating with six principal rays, hypural 2 with two, and hypural 3 with five.

DISCUSSION

Ecology of African Pellonulinae. Relatively little has been published on the ecology of African Pellonulinae. Poll (1953) and Coulter (1962) gave some information about *Limnothrissa* and *Stolothrissa,* the two genera endemic to Lake Tanganyika (Tanganyika is the only East African lake with endemic clupeids). Reynolds (1970; 1971) reported on feeding habits and schooling and migration of *Pellonula* and *Cynothrissa* in man-made Volta Lake in Ghana. The ecology of Pellonulinae in the Congo basin is unknown, excepting brief remarks on food or general habitat by Gosse (1963) and Matthes (1964).

Stolothrissa feeds on zooplankton. Juvenile *Limnothrissa* feed on zooplankton, but adults are macrophagous and evidently feed to some extent on larval *Stolothrissa. Stolothrissa* are apparently the only food of the endemic centropomid *Luciolates* (Poll, 1953). Some riverine Pellonulinae are insectivorous to a greater or lesser extent. Mature *Povilla* (Ephemeroptera) nymphs were the dominant item in the food of *Pellonula* in Volta Lake, with terrestrial insects and aquatic stages of Diptera contributing significantly to the rest of the food taken by them (Reynolds, 1970, table 1 on p. 578). Of the Congo species, *Potamothrissa obtusirostris* feeds largely on aquatic insects, *Nannothrissa parva* on phytoplankton (unicellular algae, diatoms) and zooplankton (entomostracans), and *Odaxothrissa losera* on shrimps, *Povilla* nymphs, and small fish (mainly other clupeids) (Matthes, 1964).

The West African *Cynothrissa* (which superficially resembles *Odaxothrissa*) is piscivorous, feeding largely on *Pellonula* in Volta Lake (Reynolds, 1970).

Reynolds (1971) found that *Pellonula* was among several small species in Volta Lake that migrate upwards [and shorewards?] at night in mixed aggregations, and compared this migration to that of *Stolothrissa* and *Limnothrissa* in Lake Tanganyika. It should be noted that a similar phenomenon occurs in the Pellonulinae of the Congo basin. *Poecilothrissa, Microthrissa royauxi, Potamothrissa,* and *Odaxothrissa* evidently migrate upwards or shorewards at dusk in aggregation with other small fishes, principally the cyprinids *Chelaethiops, Engraulicypris* and *Leptocypris,* and the schilbeids *Parailia* and *Pareutropius.* These aggregations apparently do not remain close to the shore all night long, but reform there for another short period around dawn. Reynolds (1971) discusses the selective advantages of such diel migrations, which are evidently primarily improved feeding opportunities, coupled with predator avoidance and possibly a metabolic advantage in living at lower temperatures and feeding at higher ones.

Thrattidion was collected only at dusk and dawn, by dipnetting in water two to three feet deep flowing swiftly along the low retaining wall that extends for about a mile above the hydroelectric dam on the Sanaga River at Edea. The only other fishes caught with it were small characids, tentatively identified as juvenile *Alestes* and *Virilia.* Its stomach contents included much unidentified material and some terrestrial insects (either Diptera or Hymenoptera) (kindly identified by Dr. David Rentz).

The larval stage of Pellonula. The only other species of Clupeidae known or likely to occur in the Sanaga River much above its mouth are *Pellonula* and *Cynothrissa.* Although adults of these genera can be distinguished, they evidently are closely related. Distinguishing characters for the juveniles have not been reported. Svensson (1933) described larvae of *Pellonula* from the Gambia River. I have collected similar juveniles in the Tano River and in the Sanaga River along with adults of *Pellonula,* and am inclined to believe that they are the same species. They are radically different from *Thrattidion.* The larvae and juveniles of *Cynothrissa* are yet to be described; presumably they are similar to those of *Pellonula.* There can be little doubt that *Sierrathrissa*

(Audenaerde, 1969), from Sierra Leone, is based on the larvae of either *Pellonula* or *Cynothrissa*. My specimens of larvae from the Tano and Sanaga rivers agree in almost all respects with the figure and description of *Sierrathrissa* except that they have more vertebrae (24+17 instead of 19+17) and are incompletely scaled (scales present only immediately behind head and on caudal peduncle). Audenaerde reported "approximately 37–38 scales in a longitudinal line, about one scale row for each body segment, scales hardly visible on posterior part of body in largest specimens." Svensson (1933: 47–48, fig. 16) describes the larva of *Pellonula* (identified as *P. vorax*) and its metamorphosis. His description of the larva agrees very well with that of *Sierrathrissa*. Concerning the metamorphosis, we may quote Svensson:

> When the fry is about 30 mm. long, an obvious and rapid change takes place in its appearance. The transparency disappears, and pigment commences to develop on the back; the head and the anterior part of the body grows thicker and higher, and the dorsal fin advances forwards so that its front part becomes situated above, or slightly behind, the vertical of the origin of the ventral fins. The gill-rakers increase in number to 25 (they are 25–30 in the adult fish, according to Boulenger) and the number of rays in the pectoral and ventral fins, as well as in the branchiostegal membrane, increases to that in the adult. It may be presumed that those changes represent a kind of metamorphosis, corresponding to that in other *Clupeids*, and in *Elopids*, and *Albulids*.

Svensson found that larval *Pellonula* have nine to ten pectoral rays, seven pelvic rays, rudimentary abdominal scutes, about 14 gill rakers on lower part of first arch, and only three branchiostegal rays visible (in specimens stained with alizarin). He did not mention the presence of scales. Adult *Pellonula* have 14 pectoral rays, eight pelvic rays, 12–14 prepelvic and eight to nine postpelvic abdominal scutes, all strongly serrate and with lateral arms, 27–32 gill rakers on the first gill arch, and six branchiostegal rays. Despite statements to the contrary (Ridewood, 1904; Poll, 1964, table 1 opp. p. 29), adult as well as larval *Pellonula* bear numerous fine teeth on the maxillary bone (Regan, 1917; personal observation). The supramaxillary bone is well developed in both adults and larvae.

Concerning other African Pellonulinae, *Limnothrissa* and *Stolothrissa* undergo profound changes in morphology from eight or ten to 25 mm, including considerable forward migration of the dorsal fin (Poll, 1953). *Microthrissa miri,* from the Niger and Chad basins, has a slender larva in the metamorphosis of which the dorsal fin position changes relatively little (Daget, 1954: 66–67, fig. 12; Blache, 1964: 58–59, fig. 21 on p. 418). Development is direct or nearly direct in at least some riverine Pellonulinae of the Congo basin. *Thrattidion* has direct development: specimens as small as 12 and 14 mm have the main features of the larger specimens, including full or nearly full complements of abdominal scutes, scales, fin rays, branchiostegal rays, gill rakers, and teeth. Fin placement remains unchanged. The most notable change is a regular increase in depth of body from 4.7–5.0 in 10–11-mm specimens to 3.55–4.1 in 19–21-mm specimens (Table 1), at which size *Thrattidion* is deeper bodied than any other African freshwater clupeid.

Systematic status of Congothrissa. In erecting a new family for *Congothrissa,* Poll (1964) stressed its 1) lack of prepelvic and postpelvic abdominal scutes; 2) unkeeled pelvic scute [with branched lateral arms]; 3) terminal mouth; 4) lack of supramaxillary; 5) short lateral [medial?] branch of supraorbital canal; 6) relatively large scales; and 7) low branchiostegal ray count. Characters 1, 4, 6, and 7 are loss or reduction characters such as one commonly finds in teleosts of greatly reduced size. Reliance on such characters leads to classifications in which the smallest representatives of a group are placed in either monotypic or polyphyletic taxonomic categories. Reduction of scutes has occurred in many lines of clupeoids. *Thrattidion* has also lost the supramaxillary. The branchiostegal ray count of *Thrattidion* (5,5 or 5,4) is intermediate between that of *Congothrissa* (3,4) and other Pellonulinae. *Congothrissa* has about 24 scales in a lateral series (Poll, 1964, table 1; fig. 1 opp. p. 8). Judging from the figure of *Congothrissa,* it may have 25 scales in a lateral series, since there are usually deeply embedded scales immediately behind the head that are not externally visible in Pellonulinae. Some specimens of *Poecilothrissa* have as few as 28 scales in a lateral series (personal observation). An unkeeled pelvic scute with branched lateral arms similar to that in *Congothrissa* is found in *Thrattidion.* I find nothing in the nature of the supraorbital canal of *Congothrissa* to distinguish it from other Pellonulinae. A terminal mouth occurs in *Thrattidion* and in some of the Congo Pellonulinae.

In conclusion, *Congothrissa* does not merit placement in a family by itself. It may either be placed in a separate subfamily, Congothrissinae, or preferably in the Pellonulinae. Its closest relatives are to be sought among the Pellonulinae in the Congo basin.

Systematic status of Thrattidion. Several of the distinguishing characteristics of *Thrattidion* — absence of supramaxillary, toothless maxillary, reduced squamation and scutellation, and low branchiostegal and gill raker counts — are loss or reduction characters more or less shared with *Congothrissa.* On the other hand, *Thrattidion* has more vertebrae (45–47), anal rays (23–25), and epurals (three) than are recorded for almost any other African Pellonulinae (*Microthrissa royauxi* has as many as 24 or 25 anal rays), and is relatively deeper bodied than any of the others at comparable size. If Congothrissinae is recognized, then a separate subfamily might also be justified for *Thrattidion.* It is preferable to place them both in the Pellonulinae.

Relationships of Dussumieriidae. Whitehead (1963b) advanced a theory with important implications for clupeoid phylogeny, namely, that Dussumieriidae are modern representatives of a primitive group of scuteless clupeoid. This theory is strongly contraindicated by the following considerations:

1) All Dussumieriidae have at least a pelvic scute that is apparently homologous with the prepelvic and postpelvic scutes in other clupeoids.

2) Several dussumieriids have either prepelvic or postpelvic scutes or both: *Etrumeus* (subfamily Dussumieriinae) has a postpelvic scute immediately behind, and partially overlapping, the pelvic scute (Chapman, 1948, fig. 17 of *E. micropus* on p. 38; personal observation); *Gilchristella* and *Ehirava malabaricus* (subfamily Spratelloidinae) have prepelvic scutes, unkeeled but with lateral arms, and no postpelvic scutes (Whitehead, 1963b; and Poll, Whitehead, and Hopson, 1965: 286); and *Laeviscutella,* which Poll, Whitehead, and Hopson placed in the same tribe with *Gilchristella* and *Ehirava,* has both prepelvic and postpelvic scutes. In *Laeviscutella* the prepelvic scutes have lateral arms but are unkeeled, whereas the postpelvic scutes are keeled but lack lateral arms, a condition unlike that in any other clupeoid.

If the absence of prepelvic and postpelvic scutes is a primitive character in those Dussumieriidae lacking them, then such scutes must have originated independently in several lines of clupeoids, including Indo-Pacific Engraulidae and two subfamilies of Dussumieriidae. It seems more likely that the ancestors of living clupeoids had a more or less full complement of scutes, and that they have been reduced or lost to varying degrees many times. A strong trend to reduce scutellation is evident in Pellonulinae. So far as known, the pelvic scute is retained in all living clupeoids. Whitehead (1963b) suggested that the pelvic scute of Dussumieriidae originated from pelvic splint bones, independently of prepelvic and postpelvic scutes. Greenwood (1968: 256) rejected a pelvic splint origin for the pelvic scute, largely on the ground that the pelvic scute is morphologically so similar to the other abdominal scutes. In *Thrattidion* the ontogeny of the pelvic scute is similar to that of the others, and the pelvic splint bone (usually absent in clupeoids) is quite separate.

While placing *Laeviscutella* in the dussumieriid tribe Ehiravini on account of its reduced scutellation, Poll, Whitehead, and Hopson (1965: 286–288) also cited reasons why it might be placed in the Clupeidae, and specifically in Pellonulinae. Daget and Iltis (1965: 45) placed it in the Clupeidae because "the only known species of *Laeviscutella* is in reality very close to the forms of *Pellonula* with which it is easily confused." In my opinion *Laeviscutella* should be placed in the Pellonulinae. Other genera currently placed in the Ehiravini also may have close relatives in the Pellonulinae. Thus the scuted *Pellonulops,* from Madagascar and South Africa (cf. Smith, 1954: 90–91, fig. 110), looks as if it might belong to the Pellonulinae and at the same time be closely related to *Gilchristella* and *Sauvagella.*

Whitehead's main reason for considering the Dussumieriidae a primitive type of clupeoid, apart from their lack of scutes, is the high number of branchiostegal rays in the subfamily Dussumieriinae, and a belief that reduction in number of branchiostegal rays is a major trend in clupeoid evolution. The notion that the number of branchiostegal rays can be reduced but not increased in teleostean phylogeny is one that had some currency formerly but has lost ground in recent years. Rosen (1964) mentions several phyletic lines in Acanthopterygii in which the number of branchiostegal rays has increased. Increases — some quite striking — surely have occurred in various highly specialized lines of catfishes in South America and India (personal observation), as well as in eels. Reduction of branchiostegal rays, of course, is the more usual trend, very frequently associated with reduction in body size, as it surely is in *Congothrissa* and *Thrattidion*. The high number of branchiostegal rays in Dussumeriinae is probably due to specialization rather than retention of a primitive character. The more pellonulin-like Spratelloidinae have only six or seven branchiostegal rays.

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